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Pollination and dispersal in Mediterranean umbellifers

Abstract

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The simple flowers of the *Umbelliferae*, organized in a characteristic inflorescence, appear unspecialized for pollination by a large variety of insect taxa. However, isolating mechanisms exist and protandry is widespread. Dichogamy is often related to petal size, the conspicuousness of the umbel, the presence and number of functionally male flowers, and pollen-grain size. This complex character syndrome is related to the breeding system and to the degree of inbreeding or outbreeding. Although the flowers show few features useful for the taxonomist, a wide array of valuable structures occur in the fruits. Many of these appear to have evolved for mericarp dispersal, both by wind and by animals. Heterocarpic taxa exist in several species, where spiny mericarps appear to serve for the spreading of the species, while non-spiny, tuberculate ones maintain the existing population.

Introduction

My work on the floral biology of the *Umbelliferae* was triggered by Bell's (1971) paper, given at a symposium on "the Biology and Chemistry of the *Umbelliferae*" held at Reading in September 1970, entitled "Breeding systems and floral biology of the *Umbelliferae*, or evidence for specialization in unspecialized flowers". Much work has been done since then, but there are still many areas awaiting study.

Often a typical umbellifer, such as *Ammi visnaga* L., can be seen with large numbers of visitors, from a wide array of taxa, seeking nectar or pollen. The tiny flowers, massed into characteristic, showy inflorescences, are successful: large numbers of viable seed, or rather, mericarps are produced.

Floral secretions

Most species seem to have a floral scent, but so far this seems not to have been studied. A recent checklist of volatile scent compounds isolated by head-space techniques (Knudsen & al. 1993), spanning the years 1966-1992, reveals no published data on *Umbelliferae*, although 700 compounds have been identified from 441 taxa in 174 gen-

era and 60 families of plants. This is an area of research that Jeffrey Harborne hopes to follow up at Reading in the near future.

Bell (1971) postulated that the American *Angelica triquinata* Michx. secretes narcotics causing insect visitors to wander haphazardly over the umbel, pollinating the flowers before falling to the ground, only to recover and fly back to another umbel to continue the process. Unfortunately, no evidence for the production of narcotics has been reported, but then no further work seems to have been carried out (Harborne, personal communication). Eisikowitch (personal communication) has found ethyl alcohol, produced by yeast cells, in *Asclepias* nectar.

However, superficially, the members of this family seem to be thoroughly promiscuous in their pollination (Bell 1971).

Characters correlated with the breeding system

In *Daucus carota* L. variants are commonly found with a single, central, dark, almost black flower, usually much larger than the rest, and arising singly with the rays of the umblets, not from an umblet itself. This does seem to be successful as acting as a decoy to attract pollinators, as Eisikowitch (personal communication) has found from careful experimentation with flies. The only other work on these flowers seems to have been by Harborne (personal communication) who has examined and identified the anthocyanin pigment present. Other variants of *Daucus* exist, though they are rare, where all the flowers in the central umblet are dark, giving a very dramatic image. *Artemisia squamata* L., from Georgia, Turkey and the Middle East, seems to adopt a similar strategy. Cullen (1972) reports that the central flowers of the umbel are sterile and form a tuft of blackish or purplish bristles. Certainly, they do have the appearance of a shaving brush. Bell & Lindsey (1978) comment on this situation and also on the presence of radiate petals, the latter phenomenon perhaps more striking in *A. squamata* than in any other species of Umbellifer. *Orlaya grandiflora* (L.) Hoffm. and *O. daucorlaya* Murb. also exhibit this phenomenon, where the outer petals of the outer umbels are many times larger than the inner. There are many more examples, though less spectacular, including *Coriandrum sativum* L. and *Heracleum* species.

The opposite extreme to showy umbels can be found in such taxa as *Hydrocotyle*, *Naufraga balearica* Constance & Cannon and *Torilis nodosa* (L.) Gaertn. The umbels are pseudo-lateral, often hidden among the leaves and subsessile, while the flowers are small, inconspicuous, the petals greenish-yellow in colour, rather than brilliant white, yellow or blue. *Bupleurum lateriflorum* Coss. from the High Atlas in Morocco has a terminal umbel and numerous, small lateral umbels along its leafless stems. Owens (unpubl.), in his doctoral thesis, examined these features for *Daucus* and related genera in the tribe *Caucalideae*. He found that inbreeding and outbreeding were correlated with a complex character syndrome. The same situation occurs in *Torilis* (Jury 1986). Koul & al. (1989) have come to similar conclusions, and also correlated the degree of inbreeding vs. outbreeding with chiasma frequency. Recent work by Koella (1993) includes some umbellifers, but is too general to come up with significant conclusions for the family and

lacks details on breeding systems. Ignorance of pollination and breeding systems has often resulted in poor taxonomy.

Torilis arvensis (Huds.) Link varies from a dwarf (15 cm), much-branched annual cornfield weed in Britain with three to four rays to the small umbels and tiny petals, to a large (2m or more), moderately branched hedgerow variant in southern Europe with up to 20 rays to the umbels, radiate petals, and a much more showy appearance. These large variants have been referred to *T. arvensis* subsp. *neglecta* (Schult.) Thell., and exhibit a much greater degree of outbreeding. Also correlated with outbreeding are the character states outer calyx teeth longer than inner, and long stamen filaments and styles. The styles often elongate considerably after anthesis.

Most umbellifers exhibit a degree of protandry, though protogyny occurs in the genera *Hydrocotyle* and *Sanicula*. Some *Chaerophyllum* species appear to be only weakly protandrous, while, as Bell (1971) reports, *Eryngium* only looks as though it were protogynous, the long styles appearing several days before the anthers open, but the stigmas not becoming receptive until the pollen has been shed. Where protandry is weak, geitonogamy (i.e. fertilization with pollen from other flowers of the same plant) occurs.

Many species show a pronounced sequence in the opening of flowers. Plants of *Magydaris pastinacea* (Lam.) Paol. were observed in Sicily at several stages. Only some time after pollen had been shed and the styles become receptive, in the primary umbels, did the flowers of the secondary umbels open, making a new supply of pollen available and providing the possibility of geitonogamy for those earlier flowers not already pollinated. "Seed-set" on most plants was 100 %.

Very many species of *Umbelliferae* are andromonoecious, with hermaphrodite and (functionally) male flowers, in which rudimentary styles and ovaries may still be present. This gives a greatly increased supply of pollen. Lovett Doust & Harper (1980) have reported on the resource costs of gender and maternal support in the andromonoecious umbellifer *Smyrniium olusatrum* L. The ratio of male to hermaphrodite flowers varies from species to species, and also dramatically between the different orders of umbels. Lovett Doust (1980) reports a ratio of male to hermaphrodite flowers of 4 : 1 in four andromonoecious species, including *Smyrniium olusatrum*. Primary, terminal umbels may contain hermaphrodite flowers only, although, at the other extreme, *Artemisia squamata* has only a few arranged around the edge of the umbel. However, in general, secondary umbels have a much higher percentage of male flowers, while tertiary ones may be composed entirely of male flowers. These trends in andromonoecious umbellifers were recognized by Knuth (1906-1909), Bell (1971), and more recently Lovett Doust (1980).

Outbreeding species often have as many as 70 % male flowers in the terminal umbel, and pronounced protandry. Also correlated with outbreeding are larger pollen grains and greater pollen production. However, it is perhaps wrong to speak of inbreeders or outbreeders, for in many cases it is the degree of inbreeding or outbreeding that we are talking about. The extreme outbreeders must be the dioecious species, such as *Trinia glauca* (L.) Dumort. Webb & Lloyd (1980) and Webb (1979, 1981) have recently studied some New Zealand taxa of diclinous apioid umbellifers, noting that all produce more flowers per male inflorescence than per female, and in all species except one, more inflorescences are produced by males than by females. Richards (1986) reports Webb &

Lloyd's view that these male-predominant ratios are due to the superior survival of male genets with their lower reproductive loads. But surely, as Richards comments, are they required to produce an adequate supply of pollen to ensure that enough pollinations take place for survival?

Insect vision is very different from ours. Implications of flower colour for visitors has been reviewed by Richards (1986). Ultra-violet light reflectance has been studied in umbellifers, but no positive results found (Bell & Lindsey 1978), though Thorp & al. (1975) reported very intense fluorescence for *Daucus carota* nectar and weak fluorescence for the pollen. However, blue is known to be a popular flower colour with bees and butterflies, and is exhibited by many *Eryngium* species where the involucre bracts serve as an attractant, perhaps less so in *E. bourgatii* Gouan and *E. triquetrum* Vahl, where the stem appears to take over this function! However, some species of *Eryngium* do not show this blue coloration, e.g. *E. campestre* L and *E. barrelieri* Boiss. What has happened there? Are these inbreeders? It should be noted that some *Eryngium* species in cultivation have strongly scented flowers and are particularly attractive to bees.

However, yellow flowers are much more frequent in umbellifers, and many examples could be quoted. Again, yellow flowers are popular with bees. *Pastinaca sativa* L. is always swarming with beetles, and there appears to be a degree of pollinator specificity. Again, more research is needed: Faegri & Pijl (1979) make very few references to the *Umbelliferae*.

Fruit dispersal

Numerous species of *Umbelliferae* have adopted the strategy of wind dispersal, with prominent wings on the secondary or vallicular ridges, e.g. *Thapsia* (lateral ridges) and *Laserpitium* (lateral and dorsal ridges). *Artedia* has extraordinary fan-like wings arranged around the edge of the dorsiventrally flattened fruits. In many instances, e.g. *Heracleum*, wings are not present as such but the whole fruit so flattened, yet relatively large, that the whole mericarp may function as a wind-dispersed unit. Other genera, such as *Ammodaucus leucotrichus* (Coss. & Durieu) Coss. & Durieu and *Cuminum setifolium* (Boiss.) Koso-Pol., have fruits covered by long, fine bristles, which must also enable wind dispersal. *Cachrys sicula* L. possesses cavities in the pericarp and is mentioned by Pijl (1982) in his book on dispersal in higher plants under the heading "balloons".

Pseudorhiza pumila (L.) Grande, from coastal sands, has fruits with stout spines on the secondary ridges, easily attached to animals and humans, especially socks and beachwear! *Caucalis platycarpus* L. also has fruits with spines. The spines in *Pseudorhiza* have numerous backwardly directed barbs at their apex, while in *Caucalis*, they are bent over to produce a formidable hook.

Daucus carota is a highly variable and complex species in need of considerable study. Inland *D. carota* subsp. *carota* seems to hybridize with subsp. *sativus* (Hoffm.) Arcang., the cultivated carrot, while around the coast numerous ecotypes exist, many of which have been recognized at the subspecific level. These also grade into *D. carota* subsp. *carota* clinally as one passes inland. The coastal plants are stout variants with spreading branches, so they are often wider than tall, are hirsute or hispid, etc. However, the main

difference appears to be in the umbel which remains flat when the fruit is ripe, whereas in inland *D. carota* subsp. *carota* the umbels contract dramatically at maturity, and show hygroscopic movements: as the relative humidity decreases, the umbels open; as it increases, they close. This has been reported by Lacey (1980) and Lacey & al. (1983). Lacey (1981) has also studied how the mericarps are transported, dropping them onto animals and measuring the distances they can be blown. She concluded that they are dispersed both by animals and the wind, as was to be expected from the morphology of their spines, again with glochidiate tips. Lacey also investigated the timing of seed dispersal in SE Michigan and the effect of parental flowering and dispersal times on offspring fate (Lacey 1982, Lacey & Pace 1983).

In the genus *Echinophora* the umblets have a single, central hermaphrodite flower and are surrounded by male flowers. These and the surrounding bracts close up as the fruit develops to form a “trample burr”, though I have never seen them function as such.

Torilis nodosa is unusual in having heterocarpic fruits. The outer mericarps of the umbel are spiny, while all the inner are tuberculate. Most fruits are, therefore, composed of tuberculate mericarps only. It seems that the spiny ones serve to spread the species to new areas, and the tuberculate ones to maintain the home population. This belief is supported by the fact that when collecting and cleaning seed of this species, the central tuberculate mericarps can be separated from the mother plant only with difficulty, while the spiny ones are usually already lost. Long dead plants usually have tuberculate mericarps still attached. Such tuberculate fruits are not rare in the tribe *Caucalideae*, occurring also in *Torilis arvensis*, *Caucalis*, *Daucus*, *Agrocharis*, etc. (Jury 1978, 1986).

When I first worked on *Torilis nodosa*, I obtained numerous seed samples from botanic garden seed lists. Nearly all gardens sent samples of an all-spiny variant, often previously referred to as *T. nodosa* f. *homoeocarpa* Thell., and it was clear they had obtained stocks from each other. Spiny mericarps are larger and fewer per umbel. [Seed size was considered by Hendrix (1984) and Hendrix & Sun (1989), who obtained somewhat conflicting results, noting that larger plants of *Pastinaca sativa* produce larger seeds. Some of their unexplained variation may be because they were confusing mericarps with seeds.] “Seed” of both *T. nodosa* variants was sown with a view to hybridize them, but then spiny fruits germinated consistently faster, and all specimens of the spiny variant flowered, fruited and died before a single flower appeared on the “normal”, heterocarpic plant. I also confirmed a difference in chromosome number ($2n = 24$ as opposed to $2n = 22$ in the heterocarpic variant), and leaf differences, and therefore I followed D. A. Webb’s advice to drink a bottle of “Bull’s Blood” and describe the all-spiny variant as a new species, naming it *T. webbii* Jury (1987). I believe it once had a more southerly distribution, now blurred by being spread around the Mediterranean by man and animals.

Sadly, for most species there are no data on how they are spread. *Pachytaenium mirabile* Maire & Pamp., endemic to Cyrenaica, appears to be most closely related to *Astrodaucus*. It has an umbel sessile in the centre of its leaf rosette, and other secondary umbels appressed to the ground at the end of prostrate branches. Sandwith, who collected the material at Kew, recorded that it had a characteristic hen-and-chickens appearance. The fruits do have large, squat, papillate spines on their secondary ridges.

Pseudorlaya pumila also often sends out its umbels in this way. This habit is a feature that is associated with a number of high-mountain taxa, such as *Carum proliferum* Maire from the High Atlas of Morocco.

Lereschia thomasii Boiss., endemic to Calabria, S Italy, has an inflorescence resembling that of some *Galium* species. It grows in deep shade under *Fagus* and *Abies* by water at 1400 m.

Does the long rough beak found in *Scandix* species function in the same way as the awn of cereals, whose fields it often shares? These fruits, even though they are green when young, must be "expensive" structures for the plant to produce.

More information on all aspects of reproductive biology for the family is urgently needed.

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